

Short-term climatic trends affect the temporal variability of macroinvertebrates in California ‘Mediterranean’ streams

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SUMMARY

1. Long-term studies in ecology are essential for understanding natural variability and in interpreting responses to disturbances and human perturbations. We assessed the long-term variability, stability and persistence of macroinvertebrate communities by analysing data from three regions in northern California with a mediterranean-climate. During the study period, precipitation either increased or decreased, and extreme drought events occurred in each region.

2. Temporal trends in precipitation resulted in shifts from ‘dry-year’ communities, dominated by taxa adapted to no or low flow, to ‘wet-year’ communities dominated by taxa adapted to high flows. The abundance of chironomid larvae was an important driver of community change. Directional change in community composition occurred at all sites and was correlated with precipitation patterns, with more dramatic change occurring in smaller streams.

3. All communities exhibited high to moderate persistence (defined by the presence/absence of a species) and moderate to low stability (defined by changes in abundance) over the study period. Stability and persistence were correlated with climatic variation (precipitation and El Niño Southern Oscillation) and stream size. Stability and persistence increased as a result of drought in small streams (first-order) but decreased in larger streams (second- and third-order). Communities from the dry season were less stable than those from the wet-season.

4. This study demonstrates the importance of long-term studies in capturing the effects of and recovery from rare events, such as the prolonged and extreme droughts considered here.

Keywords: drought, El Niño Southern-Oscillation, long-term data, persistence, stability

Introduction

The importance of long-term data in understanding temporally variable ecological phenomena has been emphasized in many studies (e.g. Connell & Sousa, 1983; Jackson & Füreder, 2006). The analysis of long-

term data can provide important insights into the mechanisms controlling long-term fluctuations in the abundance and distribution of organisms (e.g. Brook & Bradshaw, 2006; Jackson & Füreder, 2006). Furthermore, studies spanning only a few years may underestimate the natural variability of communities because they often miss infrequent events (e.g. 100-year floods, major fires) or long-term cycles in climate (e.g. multi-year droughts) (e.g. Eby, Fagan & Minckley, 2003; Lake, 2003). Long-term data may also be required to differentiate accurately the effects of

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natural variability (e.g. as a result of flooding or drought) from human impacts, particularly where natural variability is high (Gasith & Resh, 1999).

Temporal variation is often high in stream systems (e.g. Poff & Allan, 1995; Townsend, Dolédec & Scarsbrook, 1997a; Daufresne *et al.*, 2003), resulting from variability in habitat and flow (Robinson, Minshall & Royer, 2000; Oberdorff, Hugueny & Vigneron, 2001; Scarsbrook, 2002). Such fluctuations may be expected to be highest in areas with relatively high environmental variability (e.g. Boulton *et al.*, 1992), such as the mediterranean climate. The latter is characterized by predictable seasonal variation in precipitation and temperature, with hot, dry summers and cool, wet winters (Gasith & Resh, 1999). Although the timing of peak seasonal precipitation is predictable, the total amount of precipitation varies considerably between years. High variability between years results in disturbances that range from drought to severe spates, and may increase the annual variability of aquatic communities (McElravy, Lamberti & Resh, 1989). Similarly, the predictable wet and dry seasons result in marked seasonality in community composition and abundance (e.g. Bêche, McElravy & Resh, 2006).

Complex climatic patterns may be an important source of temporal variability in stream communities. For example, the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) often intensify natural wet and drought cycles, and have also been linked to changes in persistence, composition and abundance of stream fishes (e.g. Mol *et al.*, 2000; Puckridge, Walker & Costelloe, 2000) and macroinvertebrates (Bradley & Ormerod, 2001; Briers, Gee & Geoghegan, 2004; Durance & Ormerod, 2007). The ENSO drives complex weather patterns such as wind direction and velocity, temperature and the timing and amount of precipitation over cycles that return roughly every 3–7 years (Schonher & Nicholson, 1989), and future climate change may have uncertain effects on this cycle (e.g. Hoerling & Kumar, 2003). Similarly, year-to-year changes in precipitation produce variation in stream discharge and habitat quality and quantity, which in turn influence the composition, stability and persistence of aquatic communities, including invertebrates (e.g. McElravy *et al.*, 1989; Bradley & Ormerod, 2001; Milner, Conn & Brown, 2006) and fish (e.g. Oberdorff *et al.*, 2001; Eby *et al.*, 2003).

We examined long-term data (7, 8 and 20 years in duration) from three regions (10 sites in total) in northern California to determine: (1) whether the temporal variability of aquatic invertebrates is related to short-term climatic patterns (annual differences in precipitation and ENSO); (2) whether climatic patterns influence the stability and persistence of aquatic macroinvertebrate communities; and (3) whether community changes are discernible following periods of drought or flooding. In particular, we assessed the temporal variability of macroinvertebrate communities at several analytical scales (Rahel, 1990), including structural measures (the so-called 'aggregate' measures of Micheli *et al.*, 1999), such as richness and diversity, and multivariate assessments of species composition.

Methods

Site descriptions

Hunting and Knoxville Creeks Benthic macroinvertebrates were collected at four sites in Hunting and Knoxville Creeks (HKC) at the University of California McLaughlin Nature Reserve, California. Annual or seasonal collections were made from 1984 to 2003 at three sites (1P, 2P, 2D) in Hunting Creek, and one site in the adjacent Knoxville Creek (1D; Table 1). Detailed descriptions of the study sites are given by Resh, Bêche & McElravy (2005). Study site names indicate stream order (1 or 2) and permanence during the dry season (P = perennial, D = dry). For example, site 1P is a first-order perennial site (Table 1).

Arguably, the HKC dataset is the most consistently collected and analysed long-term information available for benthic macroinvertebrates. The same persons collected, identified and sorted all the samples over the entire 20-year study period.

Big Sulphur Creek and Blodgett Forest Annual benthic macroinvertebrate collections were made from one site on Big Sulphur Creek and from five sites (each on a different stream) at Blodgett Forest. Big Sulphur Creek is a third-order perennial stream located in the California Coast Range. A detailed description of this stream and site is given by McElravy *et al.* (1989). The sites in Blodgett Forest sites were located on five perennial streams located in mixed-conifer forest in the central Sierra Nevada mountains at the Blodgett

Table 1 Summary of physical characteristics of the study sites

	Latitude (N)	Longitude (W)	Elevation (m)	Stream order	Catchment area (km ²)	Flow	Total precipitation Avg \pm SD (CV)	Range of total precipitation (mm), years and period of record
Hunting/Knoxville Creeks (HKC) (Napa & Lake Counties, CA, U.S.A.)							605 \pm 232	289–1062
1D	38°47'56"	122°18'53"	390	1	2.1	Ephemeral	(38.4)	(1990) (1995)
1P	38°51'56"	122°24'54"	634	1	4.4	Intermittent		(1984–2004)
2D	38°48'30"	122°22'36"	348	2	29.3	Ephemeral*		
2P	38°49'45"	122°22'45"	402	2	22.1	Perennial		
Big Sulphur Creek (Sonoma County, CA, U.S.A.)							955 \pm 457	238–1518
BSC	38°48'3"	122°48'36"	415	3	35.0	Perennial	(50.6)	(1977) (1983) (1977–83)
Blodgett Forest Creeks (El Dorado County, CA, U.S.A.)							1680 \pm 619	664–2598
BC	38°54'44"	120°39'25"	1380	1	1.0	Perennial	(36.8)	(2002) (1995)
DC	38°54'21"	120°38'48"	1452	1	1.3	Perennial		(1995–2004)
DE	38°55'13"	120°40'14"	1280	1	1.4	Perennial		
GC	38°52'12"	120°38'31"	1243	2	4.9	Perennial		
MC	38°54'17"	120°38'39"	1310	1	2.4	Perennial		

*The channel from which samples are taken is ephemeral, but it is adjacent to a perennial channel.

Forest Research Station (Table 1). Detailed descriptions of these study sites are given by Resh *et al.* (2005). The five study sites were located on four first-order streams [Bacon (BC), Dark Canyon (DC), Deep Canyon (DE) and Mutton Creeks (MC)] and one second-order stream (Gaddis Creek, GC).

Benthic data collection

At HKC, benthic collections were made from 1984–2003 once (or twice in the case of site 1P) per year by taking five Surber samples (0.093 m², 0.5 mm mesh) in randomly selected riffles (with the same riffles being sampled each year) (Resh *et al.*, 2005). Annual samples were collected on 15 April (± 3 days), and additional post dry-season samples were collected on 15 August (± 3 days) at site 1P. At site 1P, 19 years of collection (1985–2003) were available from April (post wet-season); however, in two out of 19 years, the surface bed was completely dry in August and only 17 years of data were available (1985–2001) for the post dry-season.

At Big Sulphur Creek, four Surber samples (0.093 m², 0.5 mm mesh) were collected annually (1977–83) in the post wet-season (15 May \pm 5 days) in a random design, stratified to riffle and pool areas (two samples from riffles and two from pools). The same areas were sampled each year. At Blodgett Forest, five D-frame samples (1 m², 1 mm mesh) were collected annually in riffle and run habitats (in the

same 50 m reach) at each site (1995–98 and 2000–03) on 1 October (± 3 days) in the post dry-season.

For all datasets, invertebrates were usually identified to genus, with species distinguished as operational taxonomic units (OTUs *sensu* Resh, 1979); however, some non-chironomid Diptera and non-insects were identified to family or higher. At Blodgett Forest, Chironomidae were only identified to family. All samples from a site-season-habitat (e.g. all five samples from April at site 2P) were combined to create a composite sample, as the analysis focussed on inter-annual variation. Abundance data were log₁₀-transformed prior to all analyses (except where noted) to reduce the influence of extremely abundant taxa on results.

Climatic patterns

Precipitation The study areas are in a region of California with a mediterranean climate, characterized by cool, wet winters and hot, dry summers; 75–95% of the precipitation occurs between October and May. The following parameters were calculated based on precipitation data: total annual precipitation (1 October to sample date) for all sites, the amount of precipitation occurring 1-month prior to sampling (HKC and Big Sulphur Creek only), and precipitation 2-weeks prior to sampling (HKC only). At Big Sulphur Creek only monthly data were available

and at Blodgett Forest, 1-month and 2-week precipitation was always zero prior to the sampling date.

El Niño Southern Oscillation To investigate the potential impact of the ENSO on aquatic communities, we used the Southern Oscillation Index (SOI). The SOI is a measure of the standardized departure in the difference in sea-level pressure in the Pacific Ocean between measurements in Stand Tahiti and Stand Darwin. Because the autumn and early winter ENSO conditions in the tropical Pacific are most likely to affect late winter/early spring climatic patterns in California, we calculated the average SOI for September to January for each year, based on monthly data available from the NOAA Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/data/indices/>).

Physical habitat

Shear stress and discharge FST-hemisphere values (Statzner & Müller, 1989) were used to measure hydraulic forces (shear stress) along the stream bottom where samples were taken at each HKC site from 1989 to 1998; although a different number of measurements, based on variability of counts, were made on each sampling date (range 6–29, mean \pm SD = 13.0 ± 4.5), the mean value for each site-year was used in analyses. Each hemisphere measurement provides an estimate of the minimum bottom shear-stress force in dyn/cm required to move it (Statzner, Kohmann & Hildrew, 1991). Discharge was measured at the time of sampling at each site by measuring channel characteristics (width, depth) and velocity.

Data analysis

Analyses were conducted at two hierarchical levels: at the region (HKC, Big Sulphur Creek, Blodgett Forest) and at the study site (e.g. site 1P, 2P, BC, DC). In the case of Big Sulphur Creek, 'region' and 'study site' are the same, as there was only one site in this region. Furthermore, at Big Sulphur Creek habitats (riffle and pools) were analysed separately.

Temporal trends in community structure and composition: Community structure metrics To examine overall differences between the sites, we calculated the mean, standard deviation (SD) and coefficient of variation (CV as SD/mean) of four widely used community

metrics (total abundance, taxon richness, Simpson's index of diversity ($1-D$, where D is $1 - \sum p_i^2$) and % Chironomidae) for each site and for each year, separately. In this study, raw taxon richness was used because the sample area was standardized, which reduces the effects of variable sample size on richness estimates. Furthermore, Margalef's diversity, which accounts for differences in total abundance, was highly correlated with taxon richness ($r^2 = 0.77$, $P = 0.0001$). To examine patterns between these metrics and physical variables, we calculated the Spearman rank correlation between each metric and each physical and climatic variable for each site separately.

Discontinuities To detect periods of similar composition in the macroinvertebrate dataset, we used chronological clustering (Legendre, Dallot & Legendre, 1985; Legendre & Legendre, 1998), which is a non-hierarchical clustering technique based on a (dis)similarity matrix (Bray-Curtis distance) that imposes a constraint of temporal contiguity so that adjacent years cluster together. Thus, the result is a non-hierarchical partitioning of the data into homogenous groups using a given α -level (Legendre *et al.*, 1985). We used multiple α -levels (0.01, 0.05, 0.10, 0.20) to identify discontinuities in the data series of differing significance. Furthermore, we conducted *a posteriori* tests to determine the probability of fusion of non-adjacent groups, which would indicate a reversal in community structure (i.e. 'recovery' or a return to a community composition similar to one in the past). Chronological clustering analysis was performed using R-package 4.0 (Legendre & Casgrain, 2004).

Community composition and abundance Separate multivariate ordinations for each region (HKC, Big Sulphur Creek, Blodgett Forest) were used to explore temporal patterns in composition and abundance combining sites within a region (wet-season only). Data for the dry-season at site 1P was analysed separately from the wet-season because there is strong seasonality in community composition (Bêche *et al.*, 2006). Log₁₀-transformed abundance data were analysed using non-metric multidimensional scaling (NMS; Kruskal, 1964; Legendre & Legendre, 1998) with the Bray-Curtis distance metric in PC-ORD 4.27 (McCune & Mefford, 1999), resulting in four NMS ordinations (i.e. HKC wet-season, site 1P dry-season, Big Sulphur Creek, Blodgett Forest). Weighted-averaging was used

to find the average position of common taxa, defined as those taxa occurring in >50% of all samples in a region (Appendix 1). We then used Spearman rank correlation ($\alpha = 0.01$ because of multiple comparisons) to examine the relationship between each of the measured physical variables and year of sampling, and with each of the ordination axes.

Effects of climatic patterns on community variability: Stability and persistence of communities Stability was defined as constancy in composition and abundance over time in the face of a disturbing force (Connell & Sousa, 1983), also known as 'constancy' (Grimm & Wissel, 1997). In this study, wet-season floods were considered the disturbance, which varied from year to year in intensity and magnitude. Persistence was defined as the continued presence of a taxon over time (Connell & Sousa, 1983; Grimm & Wissel, 1997). Bray-Curtis distance between two adjacent years was used to calculate year-to-year stability (with relative abundance data) and persistence (with presence/absence data) (e.g. Scarsbrook, 2002; Milner *et al.*, 2006). We examined the relationship between these distance values and year-to-year changes in precipitation and SOI using Spearman rank correlation.

To examine whether directional change had occurred during the study period, we used time-lag regression analysis (Collins, Micheli & Hartt, 2000), which examines differences in measures of stability (Bray-Curtis distance) and time lags (1–19) between each observation. The Bray-Curtis distance was calculated for all pairs of sample dates for each site based on \log_{10} -transformed ($x + 1$) abundance data. Bray-Curtis distance was then regressed against the square root of the time lag between those samples. The square root transformation reduces the potential effect of the few data points at long time-lags on the regression (Collins *et al.*, 2000). Higher distance values indicate more dissimilar communities, and thus a positive relationship between distance and time-lag indicates directional change, a negative relationship indicates convergence on a previous community structure, and no relationship ($r^2 \approx c.0$) indicates either stability (constancy) or stochastic change (Collins *et al.*, 2000). A Mantel test between distance in time (time lag) and ecological (Bray-Curtis) distance with 10 000 Monte-Carlo simulations was used to determine whether the correlations obtained were significant using PC-ORD (v. 4.27).

Results

Climatic patterns

Precipitation Marked temporal trends in total precipitation were identified in each region (Fig. 1; Tables 1 & 2). For example, at HKC, total precipitation increased over the years studied (Table 2), which was a result of the dry conditions that prevailed in the first decade (1984–94) and the wet conditions that occurred in the latter decade (1995–2003) of the study. Furthermore, the study-period encompassed a 6-year period of extended drought (1987–92), when rainfall was within or close to the driest quartile over 66 years. At Big Sulphur Creek, total precipitation was not significantly correlated with year ($r_s = 0.54$, d.f. = 6, $P = 0.22$; Table 2), but 1977 was the driest year in the previous 108 years. At Blodgett Forest, there was a significant decrease in precipitation during the study period ($r_s = -0.86$, d.f. = 7, $P = 0.007$; Table 2), and 2002 was the driest year in the 31-year record. Furthermore, there were distinct differences in precipitation between sample periods at Blodgett Forest. The 1995–98 period was wet (>1 SD above the mean, except 1996) and the 2000–03 period was close to average (2000) or dry (2001–03, >1 SD below the mean).

There were differences in total quantity, timing and composition (rainfall or snow) of precipitation in each region. Total precipitation was highest at Blodgett Forest, intermediate at Big Sulphur Creek and lowest at HKC (Table 1). Furthermore, in some wet years (e.g. 1993), most precipitation fell early in the wet season (December and January), while in other dry years (e.g. 1991) most precipitation fell later in the season (i.e. in March or April; Fig. 1). The composition of precipitation at HKC and Big Sulphur Creek was 100% rainfall, whereas at Blodgett Forest, 15–20% of the precipitation occurred as snow.

El Niño Southern Oscillation The SOI indicated several strong ENSO events (El Niño and La Niña years) during and immediately prior to the study period (Fig. 1). For example, water years 1983 and 1998 were strong El Niño winters, with precipitation being 145–186% of the long-term average at HKC and 139–159% above average at Big Sulphur Creek and Blodgett Forest. In contrast, wet-season precipitation during La Niña years was closer to average.

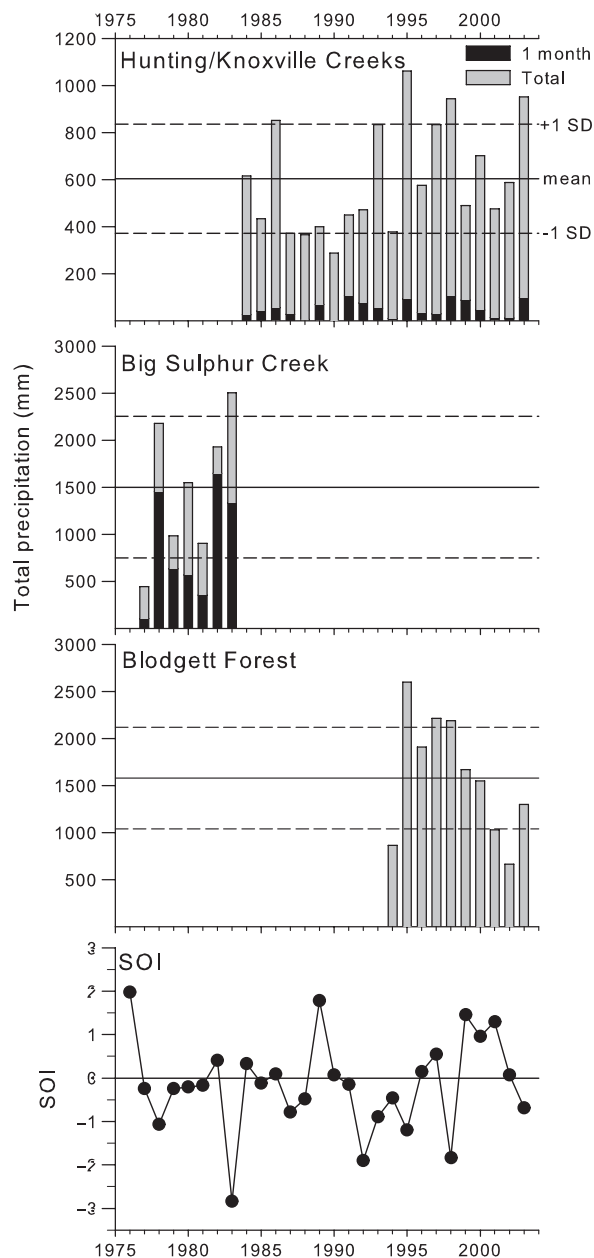


Fig. 1 Total wet season (October to sample date) precipitation (mm) (grey bars) and precipitation 1-month prior to sampling (black bars) at each study region and the mean El Niño Southern Oscillation Index (SOI from September–January; closed circles) from 1976 to 2003. 1-month precipitation was always zero at Blodgett Forest and is not included. Positive SOI indicates La Niña conditions, and negative SOI indicates El Niño conditions, with more severe events indicated by those >1 or <-1 respectively.

For example, water years 1989, 1999 and 2001 were identified as strong La Niña winters, which resulted in wet season rainfall that was 65%, 92% and 79% of

average at HKC and 85%, 106% and 65% of the average, respectively at Blodgett Forest.

Correlations between total precipitation and the SOI for the same year were not significant in any of the study regions. However, the ENSO conditions in the previous year (i.e. 1-year lag SOI) were correlated with total precipitation at Blodgett Forest ($r_s = 0.71$, $P = 0.05$; Table 2). Despite the lack of relationship between SOI and total precipitation in the other regions, SOI was significantly correlated with shear stress (FST-hemispheres, 1989–98, Table 2), and this relationship was even stronger when the sites were considered individually (data not shown).

Physical habitat

Shear stress and discharge Shear stress (average FST-hemisphere) values measured at the time of sampling differed among the sites (ANOVA, d.f. = 3, $F = 26.6$, $P < 0.001$), with highest values at site 2D and lowest values at site 1D ($2D > 2P > 1P > 1D$). Both shear stress and discharge were often positively correlated with precipitation and bed movement at each site (Table 2, site-specific data not shown). Bed movement was positively correlated with flow at Big Sulphur Creek and the Blodgett Forest sites, but not at the HKC sites, potentially because of the embedded substratum at site 2P. As expected, FST-hemispheres and discharge were significantly correlated (Table 2).

Temporal trends in community structure and composition

Long-term trends in structure metrics Measures of diversity (taxon richness and Simpson's diversity) were temporally stable at all sites and seasons, with CVs ranging between 12% and 27% (Table 3; Fig. 2). In contrast, and not unexpectedly, total abundance exhibited high temporal variability, with CVs between 68% and 87% (Table 3). Structure metrics did not exhibit consistent temporal patterns in all three regions (Spearman rank correlations between each metric and year: Table 3; Fig. 2). For example, only total abundance and % Chironomidae exhibited a significant temporal trend in more than one region (HKC and Blodgett Forest) (Table 3; Fig. 2). Temporal trends were strong for all metrics at Blodgett Forest, but this was only true for some sites (e.g. site 1P) and a

Table 2 Spearman rank correlation (r_s) among all physical variables examined

	Year	Total precip	1-month precip	2-week precip	SOI	SOI (lag)	Flow	Bed move
Hunting/Knoxville Creeks (HKC)								
Year	–							
Total precip	0.45	–						
1-month Precip	0.19	0.54	–					
2-week precip	0.41	0.54	0.46	–				
SOI	0.11	–0.25	–0.33	–0.40	–			
SOI (lag)	0.31	–0.01	–0.05	–0.16	–0.09	–		
Flow	0.32*	0.52*	0.36*	0.32*	–0.13	–0.14	–	
Bed move	0.27	0.90*	0.44*	0.26*	0.09	0.06	0.16	–
FST	0.15	0.33	0.27	0.38*	–0.33	–0.35	0.78*	0.26
Big Sulphur Creek								
Year	–							
Total precip	0.54	–						
1-month Precip	0.43	0.82	–					
SOI	0.18	–0.43	–0.05	–	–			
SOI (lag)	0.18	–0.07	–0.20	–	–0.06	–		
Flow	0.64	0.89*	0.71*	–	–0.31	0.09	–	
Bed move	0.58	0.99*	0.79*	–	–0.39	–0.02	0.94*	–
Blodgett Forest								
Year	–							
Total precip	–0.86*	–	–	–	–			
SOI	0.12	–0.34	–	–	–			
SOI (lag)	0.71	–0.71	–	–	0.43	–		
Flow	–0.22	0.22	–	–	–0.09	–0.12	–	
Bed move	–0.70	0.82*	–	–	–0.25	–0.06	0.65	–

Significant correlations are indicated in bold ($P \leq 0.05$) and/or with an asterisk ($P \leq 0.01$).

precip, precipitation; SOI, Southern Oscillation Index.

Table 3 Correlations between community summary metrics and physical variables (Spearman rank correlation, r_s) for each region, and all regions combined. (–) indicates that physical data were not available for that region

	CV (%)	Year	Total precip	1-month precip	2-week precip	FST	Flow	SOI
Total abundance								
All regions	81.5	0.04	–0.16	–0.41*	–	–	–0.23*	0.16
HKC (wet)	86.7	–0.24	–0.49*	–0.41*	–0.44*	–0.33	–0.38*	0.11
Big Sulphur Ck	67.9	–0.32	–0.64	–0.41	–	–	–0.57	0.11
Blodgett Forest	72.1	0.59*	–0.44*	–	–	–	0.06	0.09
Taxon richness								
All regions	26.5	0.35*	–0.35*	–0.54*	–	–	–0.32*	0.22
HKC (wet)	22.5	–0.07	–0.50*	–0.53*	–0.30*	–0.11	–0.14	0.09
Big Sulphur Ck	25.9	–0.16	–0.62	–0.55	–	–	–0.73*	0.15
Blodgett Forest	22.4	0.77*	–0.68*	–	–	–	0.12	0.28
Diversity (1-D)								
All regions	15.8	–0.15	–0.16	–0.21	–	–	–0.05	–0.08
HKC (wet)	12.2	–0.02	–0.01	–0.12	0.07	–0.03	0.04	0.01
Big Sulphur Ck	19.3	0.15	–0.27	–0.29	–	–	–0.28	0.07
Blodgett Forest	19.3	–0.65*	0.66*	–	–	–	0.20	–0.36
% Chironomidae								
All regions	60.0	–0.17	0.09	0.02	–	–	–0.13	0.09
HKC (wet)	68.0	–0.46*	–0.34*	–0.19	–0.34*	–0.64*	–0.49*	0.04
Big Sulphur Ck	37.4	0.47	0.59	0.51	–	–	0.71*	–0.16
Blodgett Forest	40.7	0.73*	–0.74*	–	–	–	–0.24	0.41*

Significant correlations are indicated in bold ($P \leq 0.05$) and/or with an asterisk ($P \leq 0.01$).

precip, precipitation; SOI, Southern Oscillation Index.

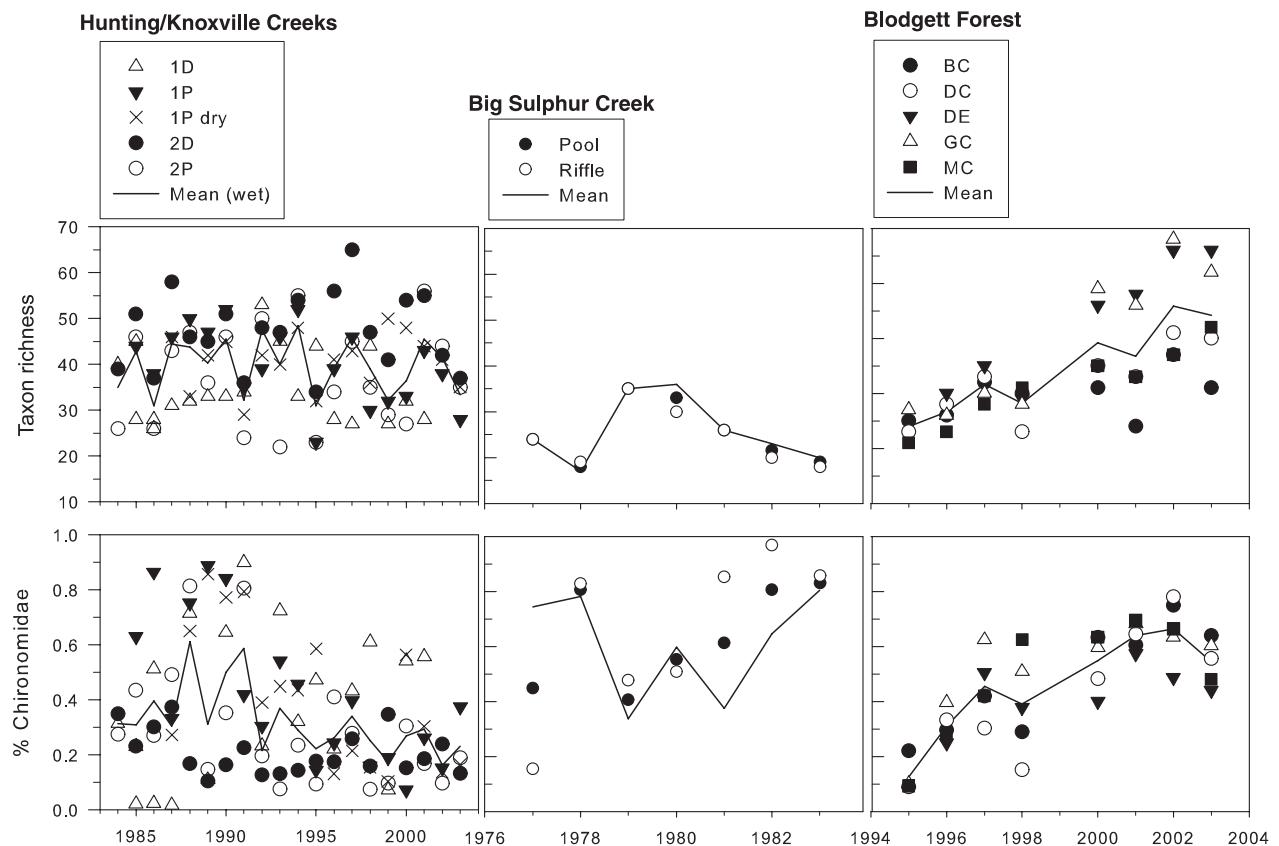


Fig. 2 Temporal trends in taxon richness and % Chironomidae for each site and the average (solid line) for each region. Site 1P dry-season is not included in the mean values presented for Hunting and Knoxville Creeks (HKC).

few metrics (e.g. % Chironomidae) in the other two regions (Fig. 2; Table 3).

Precipitation metrics were all good predictors of total abundance, taxon richness and % Chironomidae in each region. In contrast, only abundance and % Chironomidae were significantly correlated with FST-hemispheres at HKC (Table 3), and flow was not a significant predictor of any metric for Blodgett Forest streams. Simpson's diversity showed no significant correlations at HKC and Big Sulphur Creek. Furthermore, the effects of SOI on richness and diversity were mixed. For example, taxon richness decreased with SOI at site 1P dry ($r_s = -0.67$, d.f. = 16, $P < 0.01$; i.e. low richness in La Niña years), but increased with SOI at Blodgett Forest (i.e. high richness in La Niña years), and diversity decreased with SOI (Table 3).

When all regions were combined, few significant trends remained between summary metrics and physical and climatic variables. For example, flow was negatively correlated with total abundance and taxon richness for all regions, and 1-month precipita-

tion were negatively correlated with total abundance, taxon richness and diversity (Table 3).

Discontinuities in community composition and abundance **Hunting/Knoxville Creeks** Chronological clustering detected discontinuities in the multivariate time series for each HKC site ($\alpha \leq 0.20$) except site 2P (Fig. 3). Furthermore, the major discontinuities at these sites were associated with years that were before, during or after the prolonged drought period (1987–92). For example, the most significant discontinuity ($\alpha = 0.01$) was at the onset (site 1P wet and dry-season 1987) or end (site 1D, 1994; site 1P dry-season, 1991) of the extended drought period (Fig. 3). However, the shifting point in community composition ($\alpha \geq 0.05$) occurred in 1989 at site 2D, which was early in the prolonged drought (Fig. 3). Additionally, both first-order sites shared the same discontinuities when considering higher α values ($\alpha \geq 0.05$) (1987, 1991 and 1994), which represent the beginning and end of the extended drought.

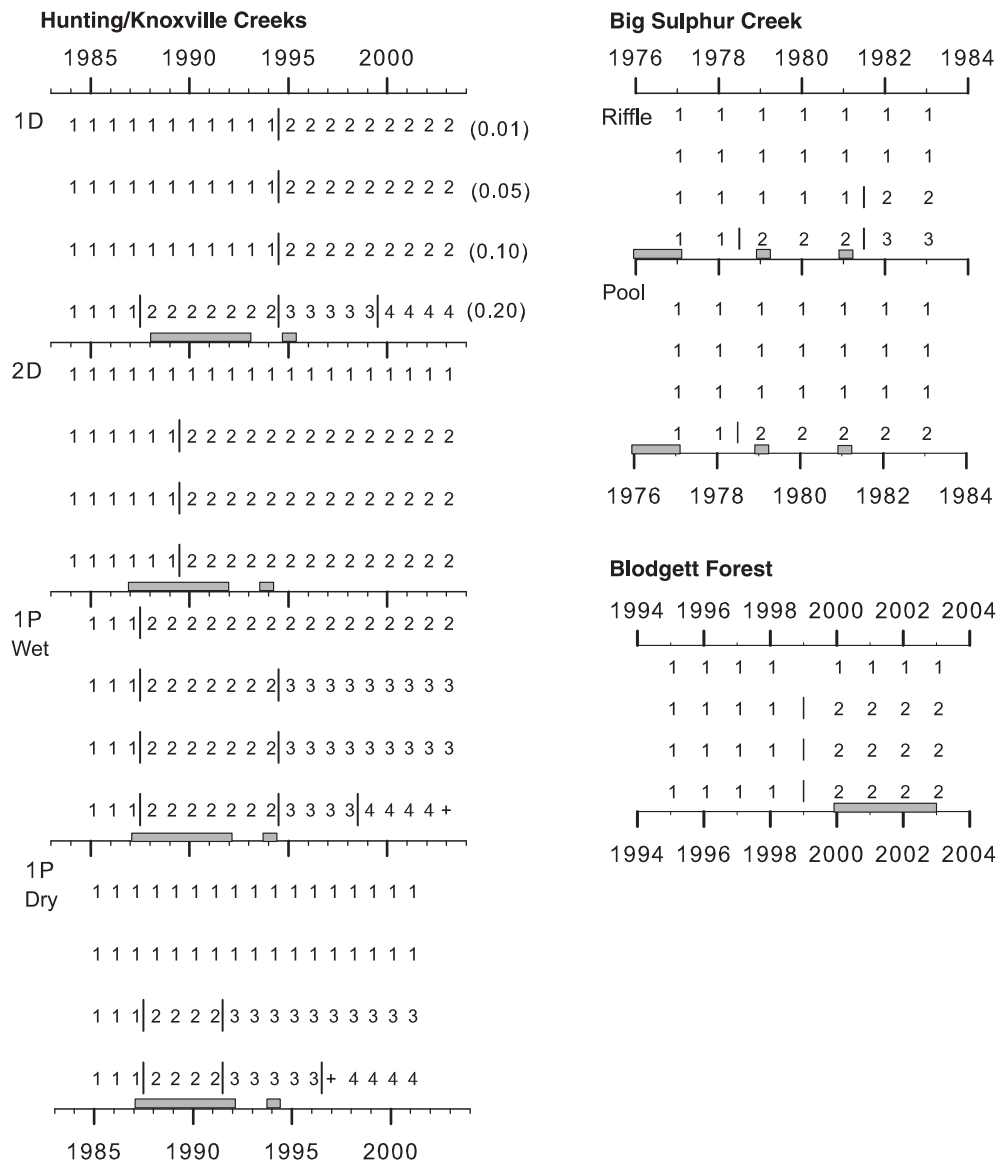


Fig. 3 Chronological clustering results for various α levels (0.01, 0.05, 0.10, 0.20). Discontinuities are indicated by different numbers for each site. There were no discontinuities identified at Site 2P. Outliers are indicated by the + symbol. Grey bars correspond to dry years as discussed in the text.

The changes in community composition and abundance were gradual, as indicated by the fact that all groups could be expanded by 1 year at a time ($P < 0.05$). For example, a group of years (e.g. 1984–89) could be expanded by adding 1 year at a time (1990 then 1991, etc.) without changing the significance of the group. In contrast, a sharp community change would be indicated by an insignificant probability of group expansion ($P > 0.05$; i.e. adding the next year to the group would make the group no longer significant). Furthermore, in cases where the

time series was divided into >2 groups (i.e. $\alpha = 0.20$ for sites 1P and 1D), convergence of community structure and composition was observed between the first and last groups (Fig. 5).

Big Sulphur Creek and Blodgett Forest At Big Sulphur Creek, discontinuities ($\alpha \leq 0.20$) were associated with extreme dry (pools and riffles) and wet (riffles) years (Fig. 3). For example, for pools, the only discontinuity identified was between 1978 (1-year post drought) and 1979 ($\alpha = 0.20$). The major discontinuity in riffle

communities separated the two very wet years (1982 and 1983) from earlier periods ($\alpha = 0.10$), and another between 1978 and 1979 ($\alpha = 0.20$; Fig. 3). Macroinvertebrate communities at all of the Blodgett Forest sites exhibited a discontinuity between 1998 and 2000 ($\alpha \geq 0.05$; Fig. 3), which was also identified in the NMS ordination (Fig. 5). Similar to the HKC results, the transitions between the periods were gradual for both Big Sulphur Creek and Blodgett Forest.

Patterns of temporal variability in macroinvertebrate community composition at Hunting/Knoxville Creek Based on NMS ordinations of all the wet-season samples combined, benthic macroinvertebrate communities underwent directional change in structure and composition at three of the four sites (1D, 1P, 2D cf. 2P) after or during the extended drought period (1987–92). A three-dimensional NMS solution represented 81.4% of the total variance for the wet-season sites (stress = 13.9, $P = 0.001$) (Fig. 4). Similarly, a two-dimensional solution represented 88.5% of the total variance for site 1P dry-season (stress = 10.5, $P = 0.001$) (Fig. 5). Considered as a region (HKC, wet-season only), axis 1 was significantly correlated with year, total, 1-month and 2-week precipitation, whereas axis 2 was significantly correlated only with year and flow (Fig. 4, Appendix 2). Axis 3 was highly correlated with shear stress and flow, which differed greatly among the sites. An ANOVA showed significant differences ($F = 33.7$, d.f. = 3, $P < 0.0001$) in mean axis 3 scores among sites. Differences between sites along axis 1 and 2 were significant, but weaker (axis 1: $F = 7.2$, d.f. = 3, $P = 0.0003$; axis 2: $F = 11.4$, d.f. = 3, $P < 0.0001$).

Community change was mainly caused by changes in the abundance of chironomids at three of the five sites and seasons. For example, % Chironomidae was significantly correlated with all NMS axes (1, 2 and 3) at site 1P ($r_s = 0.49$, $P = 0.035$; $r_s = 0.67$, $P = 0.002$; and $r_s = 0.49$, $P = 0.035$, respectively; d.f. = 18), axis 3 at site 1D ($r_s = -0.80$, $P < 0.0001$, d.f. = 19), and axis 3 at site 2D ($r_s = 0.51$, $P = 0.02$, d.f. = 19). Chironomid taxa were positively associated with early survey years (i.e. pre-drought, 1984–87) and drought years (1987–92, 1994), when % Chironomidae increased over 80% (except at site 2D).

Changes in precipitation were associated with changes in other common taxa. For example, many more taxa were associated with dry (21 taxa) than wet (five taxa) conditions at all of the sites sampled

during the wet season (Fig. 4), as determined by Indicator Species Analysis comparing 'wet' and 'average' precipitation years to 'dry' years for all sites combined. For example, the caddisflies *Hydropsyche* and *Ochrotrichia* were associated with dry years. Other taxa associated with dry years included the dipterans *Palpomyia* and seven species of Chironomidae, the caddisflies *Hydropsyche* and *Tinodes*, the beetles *Gyrinus* and *Tropisternus*, the hemipteran *Ambrysus* and the oligochaete Lumbriculidae (see also Fig. 4). In contrast, only five taxa indicated wet or 'average' rainfall years, including two stonefly taxa (*Sweltsa* and first-instar Plecoptera), two dipterans (*Blepharicera* and *Dicranota*) and the non-insect Cladocera.

Big Sulphur Creek The variation in community structure and abundance at Big Sulphur Creek was related to differences in habitat (pool versus riffle) and total rainfall (drought to wet years). The NMS of log₁₀-transformed abundance resulted in a three-axis solution (stress = 9.5, $P = 0.03$) representing 80.7% of the total variance (Fig. 4). The NMS solution shows habitat differences along axes 1 and 2, which were confirmed by multiple response permutation procedure by habitat ($A = 0.039$, $P = 0.035$). The Big Sulphur Creek NMS ordination was significantly correlated with total and 1-month precipitation, year of sampling, flow and SOI (Fig. 4). Percent Chironomidae was strongly correlated with change along axis 1 for pools ($r_s = -0.79$, $P = 0.04$, d.f. = 6) and along axis 3 for riffles ($r_s = -0.82$, $P = 0.02$, d.f. = 6).

Similar to the results from HKC, more taxa were associated with dry conditions than wet conditions in both pools and riffles (based on Indicator Species Analysis, see also Fig. 4). In particular, only one species of Chironomidae indicated wet conditions whereas six species were more common in dry years, including three species of Chironomidae, the megalopteran *Sialis* and the non-insects Acarina and Oligochaeta.

Blodgett Forest When combined, the major groupings of the NMS ordination of all sites at Blodgett Forest were related to site rather than year (Fig. 4). The NMS of log₁₀-transformed abundance resulted in a three-axis solution (stress = 9.2, $P = 0.001$) representing 91.7% of the total variance (Fig. 4). The mean ordination score for each site on each axis differed significantly

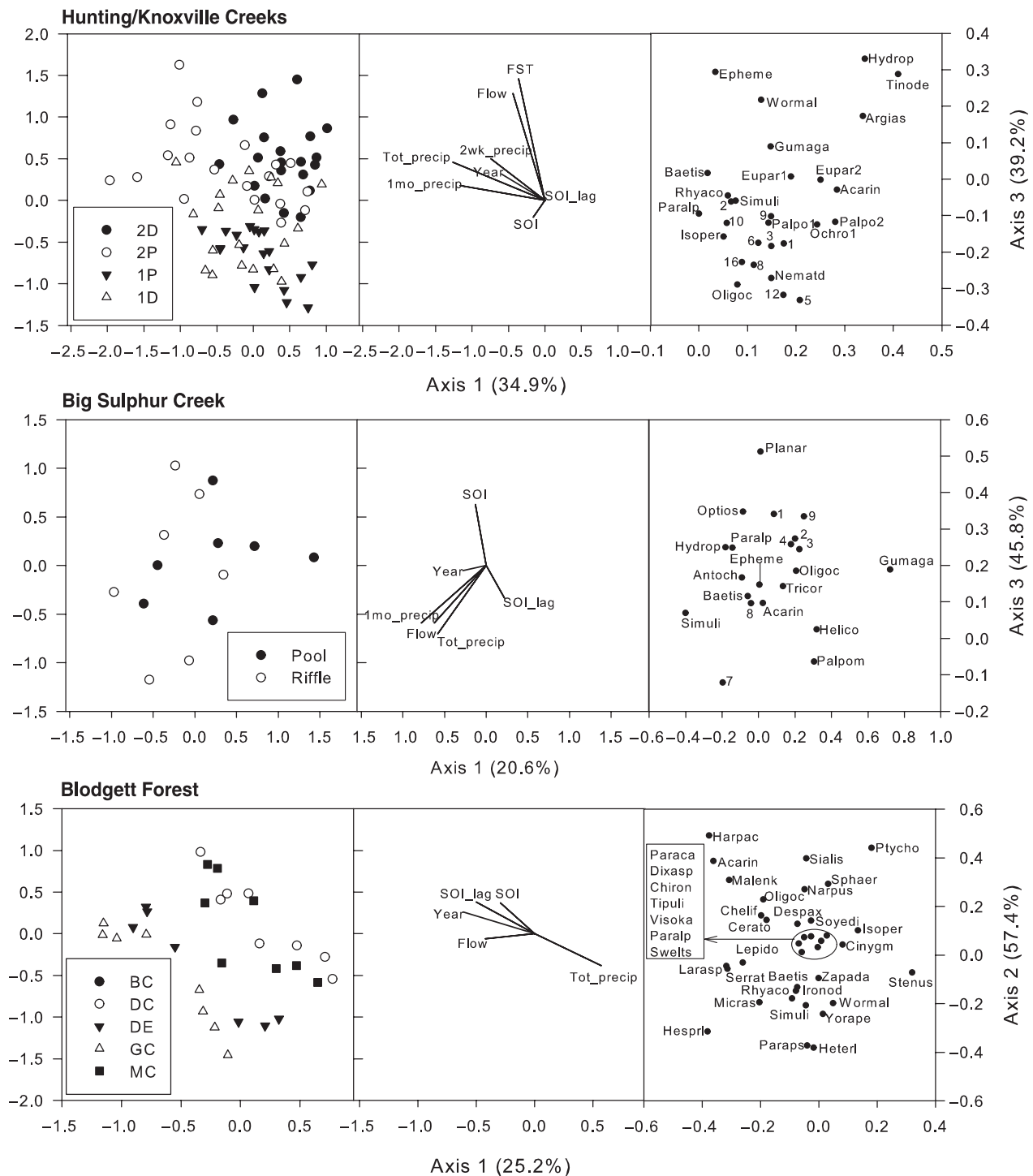


Fig. 4 NMS ordinations of \log_{10} -abundance in site-year space and taxon-space for each study region. Sites or habitats sampled within each region are indicated by different symbols. Ordination plots of taxa are based on weighted-averaging. Taxa codes are listed in Appendix 1; Chironomidae species are listed as numbers. For example '1' refers to Chironomidae sp. 1.

(ANOVA, d.f. = 4). The differences between sites were greatest along axis 1 ($F = 10.7$, $P < 0.0001$) and axis 3 ($F = 9.7$, $P < 0.0001$), and less pronounced along axis 2

($F = 4.9$, $P = 0.003$). Furthermore, axes 1 and 2 were both significantly correlated with year, total precipitation, flow and SOI(lag), whereas axis 3 was only

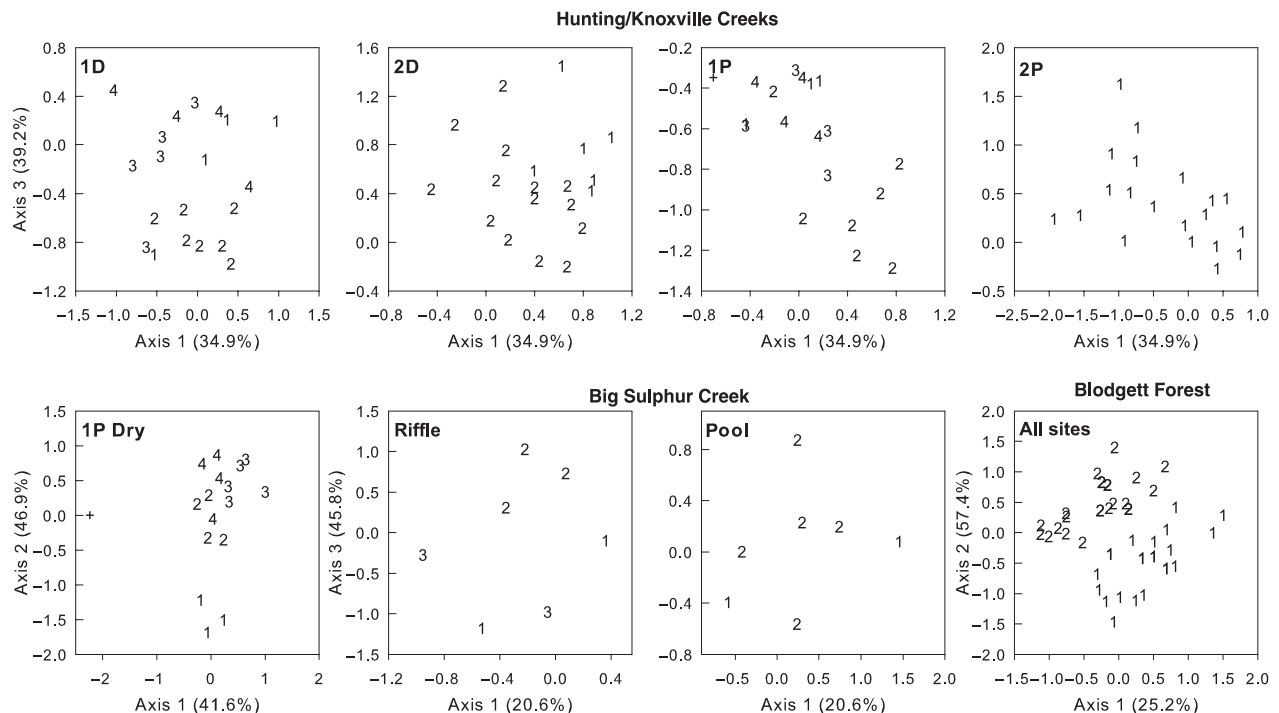


Fig. 5 NMS ordinations of \log_{10} -abundance separated by site/habitat. Ordination locations are based on regional NMS plots in Fig. 4. Here, symbols correspond to discontinuities identified by chronological clustering (Fig. 3) at ($\alpha = 0.20$), where years that grouped together have the same letter symbol. All sites and habitats are plotted separately except for Blodgett Forest sites, which are plotted together because here the patterns are not obscured.

significantly correlated with total precipitation and SOI (Fig. 4, Appendix 2). Percent Chironomidae contributed to change along axes 1 and 2 when all sites were combined ($r_s = -0.55$, $P = 0.0003$; $r_s = 0.62$, $P < 0.0001$, respectively, d.f. = 39).

As was found at Big Sulphur Creek and HKC, more taxa were associated with dry years (24 taxa) than wet years (five taxa) based on Indicator Species Analysis (see also Fig. 4). Dry year taxa included Chironomidae, the beetle *Ampumixus*, the stonefly *Malenka* and the non-insects Acarina and Oligochaeta. Wet year taxa included the dipteran *Simulium*, the stoneflies *Parapsyche* and *Zapada* and the caddisfly *Hydropsyche*.

Effects of climatic patterns on stability and persistence of aquatic communities

Stability was highest at the HKC sites (Bray-Curtis distance = 0.43 ± 0.17 , mean \pm SD) followed by Big Sulphur Creek (0.62 ± 0.23) and Blodgett Forest (0.68 ± 0.13). There were significant differences in stability between regions based on a Wilcoxon U-test ($\chi^2 = 45.1$, d.f. = 2, $P < 0.0001$). In contrast, persis-

tence was lowest at Blodgett Forest (Bray-Curtis distance = 0.24 ± 0.06), but there were no differences between average persistence at HKC (0.38 ± 0.10) and Big Sulphur Creek (0.39 ± 0.12). There were significant differences in persistence between regions (U-test, $\chi^2 = 45.5$, d.f. = 2, $P < 0.0001$).

At Big Sulphur Creek, stability and persistence was lowest between 1977 and 1978 for both habitats (although persistence was lowest between 1978 and 1979 for riffles). At Blodgett Forest, year-to-year stability and persistence was lowest between 1998 and 2000 (at four and three sites, respectively; Fig. 6).

Year-to-year stability and persistence of macro-invertebrate communities tracked ENSO for HKC and Blodgett Forest, but not Big Sulphur Creek (Table 4). For example, stability decreased with increasing SOI at HKC ($r_s = -0.25$, $P = 0.03$, all sites combined; $r_s = -0.75$, $P = 0.0004$, site 1P; Fig. 6), where negative SOI values indicate El Niño conditions. Similar patterns were also found between persistence and SOI at HKC (sites 1P, 2P and HKC sites combined, Blodgett Forest sites combined; Table 4). Persistence (site 2P, HKC sites combined,

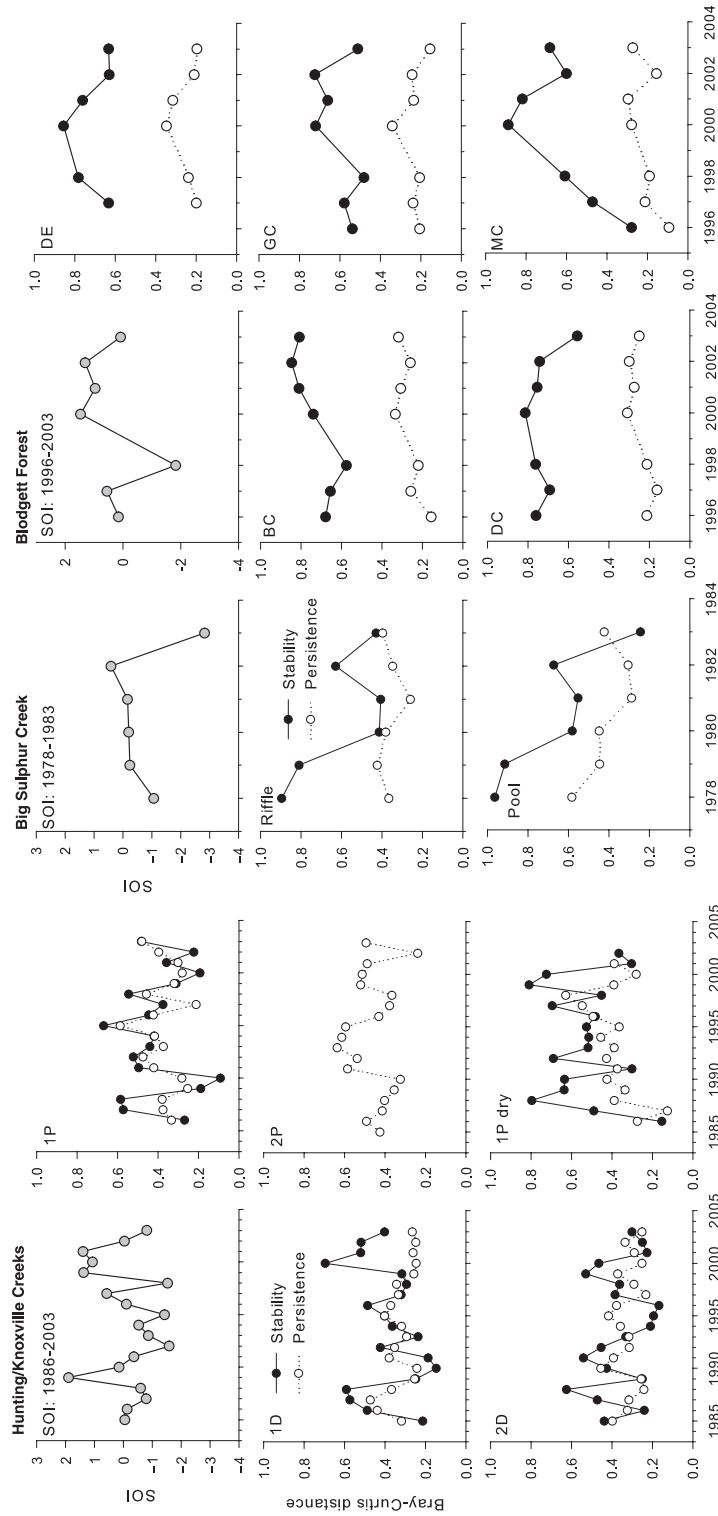


Fig. 6 Year-to-year stability (closed circles) and persistence (open circles) of macroinvertebrate communities, as measured by Bray-Curtis distance of relative abundance and presence/absence data, respectively, for each region. The ENSO index (SOI) is shown for reference (grey circles) for each region and time-period.

Table 4 Relationship between stability and persistence of aquatic macroinvertebrate communities (as measured by Bray-Curtis distance of relative abundance or presence/absence) and ENSO (SOI, and difference in SOI between years) and rainfall (total difference, and % difference between years)

	Stability					Persistence				
	SOI (begin)	SOI (end)	SOI diff	Precip (diff)	% diff precip	SOI (begin)	SOI (end)	SOI diff	Precip (diff)	% diff precip
Hunting/Knoxville Creeks (HKC)										
All sites	-0.16	-0.25	-0.07	-0.04	-0.03	-0.17	-0.21	-0.09	0.24	0.19
1D	-0.05	0.07	-0.19	0.12	-0.04	-0.06	0.00	-0.44	0.34	0.38
2D	0.11	-0.09	-0.03	-0.44	-0.29	-0.08	-0.06	0.23	0.33	0.00
1P	-0.30	-0.75	-0.16	0.16	0.17	-0.23	-0.80*	0.09	0.18	0.05
2P	-0.31	-0.19	0.26	-0.09	-0.01	-0.54	-0.38	-0.30	0.47	0.61*
1P (dry)	-0.17	0.17	0.34	-0.26	-0.42	-0.11	-0.36	0.40	-0.14	-0.13
Big Sulphur Creek										
All sites	-0.44	-0.04	0.19	0.89*	0.57*	-0.21	-0.59	0.34	0.11	0.14
Riffle	-0.37	-0.37	0.60	0.90	0.70	-0.14	-0.66	0.60	-0.02	-0.26
Pool	-0.70	0.03	0.06	0.90	0.70	-0.32	-0.54	0.09	0.26	0.54
Blodgett Forest										
All sites	0.01	0.39*	0.10	0.18	0.17	-0.10	0.46*	0.06	0.21	0.30
BC	0.39	0.29	-0.36	0.29	0.89*	-0.18	0.36	-0.04	0.25	0.11
DC	-0.32	0.18	0.75	0.18	-0.50	-0.04	0.36	0.25	0.46	0.68
DE	-0.49	0.26	0.43	0.14	-0.66	-0.03	0.54	0.37	0.26	0.60
GC	0.21	0.61	-0.07	0.18	0.39	0.00	0.61	0.18	0.07	0.64
MC	-0.11	0.32	0.11	0.11	0.36	-0.07	0.57	-0.32	0.04	0.00

Significant correlations are indicated in bold ($P \leq 0.05$) and/or with an asterisk ($P \leq 0.01$).

Precip, precipitation; SOI, Southern Oscillation Index.

Blodgett Forest sites combined) and stability (Big Sulphur Creek) were also significantly correlated with year-to-year precipitation differences (Table 4).

Directional change in community composition and abundance was observed at each HKC and Blodgett Forest site using time-lag regression analysis (Fig. 7), although the magnitude of change varied among sites. In contrast, directional change was not observed at Big Sulphur Creek, whether habitats were considered separately or combined (Fig. 7). At HKC, directional change was most pronounced in the smaller streams (sites 1P and 1D), whereas change was least directional at site 2P and intermediate at site 2D (Fig. 7). Despite low r^2 values, all of these patterns of directional change were statistically significant based on Mantel tests ($P < 0.05$), with the exception of site 2P ($P = 0.054$). Similarly for Big Sulphur Creek, when the 1977–78 comparison was removed (1977 was an extreme drought year followed by a wet year), communities from pools and both habitats combined exhibited significant directional change ($r^2 = 0.25$, $P = 0.025$; $r^2 = 0.10$, $P = 0.047$ respectively). At Blodgett Forest, directional change was strongest at sites GC, DE and BC ($r^2 > 0.60$), and weakest at sites

MC and DC ($r^2 \leq 0.60$). However, communities from all Blodgett Forest sites exhibited much stronger temporal patterns than in the other two regions.

Discussion

Much of the temporal variation in composition and abundance of the macroinvertebrate benthos in these three regions of California can be explained by short-term climatic patterns (i.e. annual differences in precipitation). Furthermore, community change was largely directional in nature, which can be attributed to temporal trends in precipitation. Here, we consider the multi-year patterns observed and the influence of short-term climatic variability (i.e. precipitation and ENSO events) on community stability and persistence.

The considerable variability in the total amount and timing of precipitation resulted in predictable changes in macroinvertebrate community composition, abundance and taxon richness in all three study regions in northern California. For example, the two best explanatory variables of macroinvertebrate communities were total wet-season precipitation (all sites) and shear stress (first-order HKC sites). Both

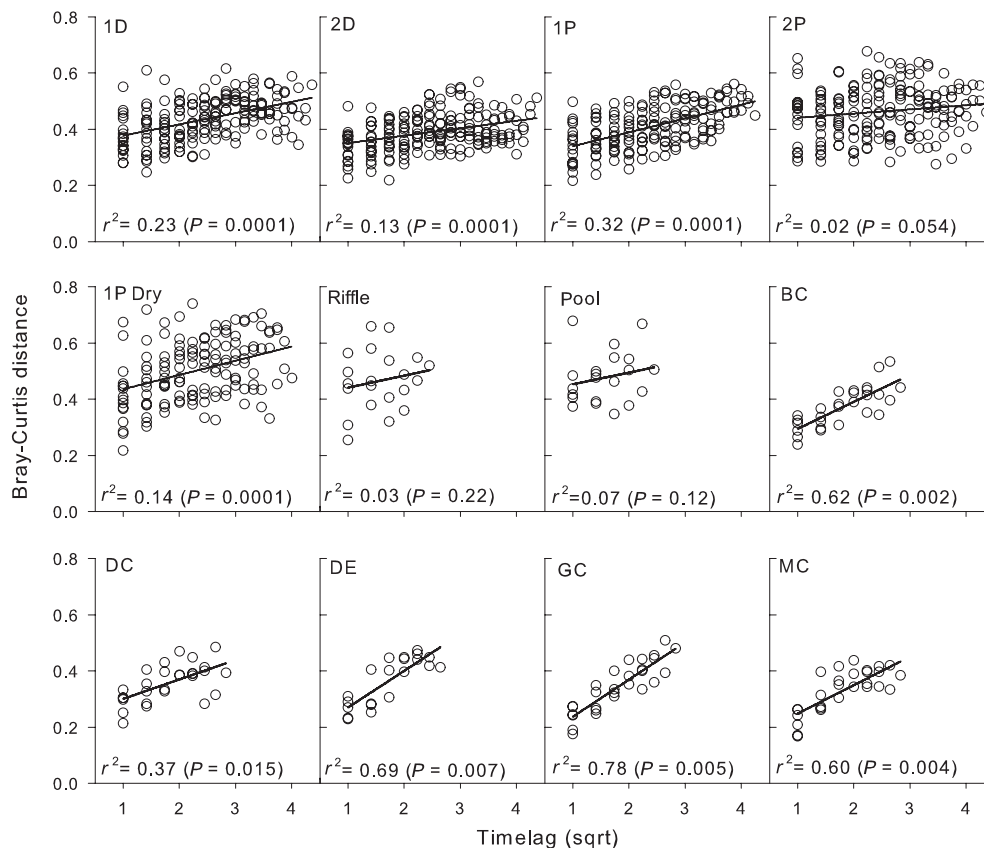


Fig. 7 Time-lag regression analysis results, showing Bray-Curtis distance between each pair of observations versus the square root of the time lag between observations for each site. r^2 values are presented based on linear regressions, and significance values are based on 10 000 Monte Carlo simulations.

of these measurements reflect year-to-year changes in hydrology that occur as a result of annual climatic variation.

Although these communities exhibited relatively low stability over long temporal scales, community variability could be largely explained by variability in climate and, thus, the habitat that resulted. The relationship between conditions immediately before (or during) sampling and community composition appears to be obscured in years where there had been ample time (e.g. >1 month) between the last disturbance (i.e. flood) and the sampling date, which allows for recolonization (e.g. Townsend *et al.*, 1997a).

Variability of community structure metrics

Of the physical habitat variables used, the majority of metrics responded most strongly to total annual precipitation. Despite relatively low CV values, taxon richness was the most sensitive metric to measures of

habitat variability. In particular, taxon richness decreased with increasing flooding (as indicated by precipitation and hydraulic metrics). Negative relationships between richness and disturbance have been frequently documented in the stream ecology literature (e.g. Death, 2002), despite some studies supporting the intermediate disturbance hypothesis (e.g. Townsend, Scarsbrook & Dolédec, 1997b).

Total abundance was also sensitive to annual differences in precipitation in all regions, despite high CVs and significant temporal trends resulting from either the linear increase (HKC) or decrease (Blodgett Forest) in total precipitation during the study period (Fig. 1). In contrast, diversity (Simpson's 1-D) was stable over time (low CVs) in all regions, despite dramatic changes in habitat. High constancy was also found when other diversity metrics were examined, such as Shannon-Weiner H' and Margalef's diversity (L. Bêche, unpubl. data), and by other studies (e.g. Robinson *et al.*, 2000). This high constancy despite

environmental variability suggests that these types of aggregate diversity metrics have limited usefulness in most ecological studies.

Variability in precipitation greatly altered the species composition and abundance of Chironomidae. This group was the most species rich and abundant of all the taxa at each site (long-term average of 21–42% of total abundance) and was responsible for much of the temporal change in community structure over time, as indicated by their increased abundance in dry years (Table 3) and correlations with ordination axes indicating temporal change. Although most chironomids responded similarly to changes in precipitation, there were several species that showed opposite responses, particularly at Big Sulphur Creek, indicating that analyses at the family level lack sufficient taxonomic resolution. In this study, the identification of chironomids to OTUs allowed us to detect changes in chironomid composition without species-level identification. This approach, however, does not allow us to use existing literature to speculate why some chironomid species responded differently than others to environmental change. Because species-specific information is sparse for chironomids, however, such an analysis would be difficult. Nonetheless, because most studies only identify chironomids to family, valuable information on shifts in composition may be missed. Thus, the accurate identification (even to OTUs) of these organisms may lead to more informative interpretations of community processes, particularly given their ecological diversity (e.g. Pinder, 1986).

An interesting consequence of the lower taxonomic resolution used for Chironomidae at the Blodgett Forest sites is that diversity (1-D) and taxon richness were *negatively* correlated with one another. This resulted in opposite trends between these two metrics and habitat conditions (Table 3). Taxon richness increased during the study period with decreasing precipitation (as it did in all regions), however, diversity decreased with increasing precipitation as a result of the increased dominance of Chironomidae. Diversity metrics are sensitive to taxon dominance, and at the Blodgett Forest sites, both the total and percentage composition of Chironomidae were dramatically affected by decreasing precipitation. Although Chironomidae were also sensitive to precipitation changes in HKC and Big Sulphur Creek (Table 3), the use of OTUs indicated that no single chironomid species dominated the community and

counter-intuitive negative correlations between richness and diversity were avoided.

Dry season communities were weakly or not related to wet season conditions for all metrics at site 1P (HKC), but not at Blodgett Forest. A lack of a relationship between dry-season communities and annual variability in precipitation was also found by McElravy *et al.* (1989) and by Feminella & Resh (1990) when examining communities and populations of *Helicopsyche borealis* (Hagen, 1861), respectively, in Big Sulphur Creek. The discrepancy between dry season communities at Blodgett Forest and HKC may be explained by the differences in their respective precipitation regimes. Snowfall at Blodgett Forest resulted in high discharge until September (sampling was in October); isolated pools never form in these streams. In contrast, rainfall at HKC usually ends by late April, and discharge is reduced to base-flow within 1 month (i.e. by June), and to isolated pools by the time of sampling in August. Thus, seasonal drying is potentially a greater stress on dry season communities at site 1P than in the Blodgett Forest streams, resulting in decreases in abundance, richness and diversity (Gasith & Resh, 1999). Differential impacts of seasonal drying between streams of differing size (smaller streams = greater impacts) were also found by Bêche *et al.* (2006).

Directional change of community structure and composition

Community variability has been shown to increase with study length in some studies, because longer time periods may encompass more environmental change (e.g. Bengtsson, Baillie & Lawton, 1997; Haddad, Tilman & Knops, 2002). In contrast, long-term (>5 years) stability and persistence of aquatic macro-invertebrate communities has been demonstrated in several different regions in the world (e.g. montane U.S.A.: Robinson *et al.*, 2000; New Zealand: Scarsbrook, 2002, UK: Woodward, Jones & Hildrew, 2002). In this study, there is more evidence to suggest the former, rather than the latter. For example, directional change was found at all sites as a result of directional patterns in precipitation, and thus flow. Furthermore, we found that the magnitude of directional change varied among the regions and individual sites. For example, directional change was most evident at site 1P (wet-season) from 1990 to 2003 (Figs 5 & 7) and can

be attributed to a vegetation encroachment (*Typha* sp. cattails) following the prolonged drought (1987–92). Vegetation encroachment increased fine sediment, narrowed and filled the channel, and raised near-bed hydraulic conditions. Similar, although less extreme, encroachment of vegetation occurred at all HKC sites during the prolonged drought. In the second-order sites (2D and 2P), intense flooding in later years uprooted some or all of this vegetation, although at site 1P encroachment it has resisted even dramatic increases in flow (e.g. in 1995).

Directional change in community structure and abundance is most often associated with community succession following disturbance or the creation of new habitat, particularly following press or ramp disturbances, such as climatic warming (Daufresne *et al.*, 2003), drought (Bady *et al.*, 2004), flow alteration (Usseglio-Polatera, 1997), or a combination thereof (e.g. flow alteration and exotic species; Eby *et al.*, 2003). In this study, there was a shift in compositional structure from 'dry-year' communities, dominated by taxa adapted to low flow conditions to 'wet-year' communities, dominated by taxa adapted to high flow or floods.

Influence of habitat variability on community stability and persistence

Community stability or persistence and habitat variability are negatively related in many aquatic and terrestrial communities (e.g. Bengtsson *et al.*, 1997; Oberdorff *et al.*, 2001; Milner *et al.*, 2006). Factors influencing habitat variability in streams include: flow regime (perennial versus intermittent), stream size and precipitation regime (rain-fed versus snow-melt). Thus, because stream flow is unpredictable and highly variable between years under a mediterranean-climate (Gasith & Resh, 1999), communities may exhibit relatively low stability compared to most other climatic regions (e.g. Moyle & Vondracek, 1985). Supporting this hypothesis, we found that communities in mediterranean streams fed by rainfall (i.e. HKC and Big Sulphur Creek) were less persistent than communities in snow-melt streams (i.e. Blodgett Forest) or in other regions with more stable flow (e.g. Robinson *et al.*, 2000; Metzeling *et al.*, 2002; Scarsbrook, 2002). Similarly, both stability and persistence were lowest between years with the greatest difference in total precipitation (high habitat variability). In

contrast, macroinvertebrate communities often have high temporal stability and persistence over 6–10 years when flow is relatively constant between years (Death & Winterbourn, 1994; Robinson *et al.*, 2000; Metzeling *et al.*, 2002; Scarsbrook, 2002; Woodward *et al.*, 2002).

All the communities examined exhibited high to moderate persistence and moderate to low stability, which suggests that although the complement of taxa did not change greatly, their relative abundance changed substantially. This pattern of high persistence but low stability has been documented frequently (e.g. Rahel, 1990) and may be expected in macroinvertebrate stream communities (Robinson *et al.*, 2000) because taxon abundances may respond rapidly to changes in habitat, food and disturbance, or may fluctuate as a result of changes in timing of life-cycle events (e.g. hatching, emergence).

Year-to-year stability and persistence of communities was also influenced by ENSO cycles, where there was higher stability and persistence during negative (cold, dry) phases of ENSO and lower stability in positive phases (warm, wet) (Table 4, Fig. 6). Bradley & Ormerod (2001) found similar relationships between invertebrates and the North Atlantic Oscillation (NAO). Other studies on the biotic effects of ENSO or NAO in freshwater have generally linked responses of organisms to changes in precipitation (e.g. Mol *et al.*, 2000; Puckridge *et al.*, 2000) or temperature (Briers *et al.*, 2004) as a result of these climatic cycles. In our study, as in that of Bradley & Ormerod (2001), the effects of climatic cycles on precipitation and temperature cannot be directly linked to many observed changes in community structure and abundance partly because our measurement of flow variability was precipitation-based. Additionally, the effects of ENSO on climate (temperature, precipitation) are complex (Schonher & Nicholson, 1989), such that not all El Niño years result in dramatic increases in precipitation (see Fig. 1). Therefore, the effects of climatic cycles such as the ENSO and NAO may also be distinct from other variations in climate. For example, Durance & Ormerod (2007) demonstrated that climate change (temperature increase) and NAO climate cycles have distinct effects on stream macroinvertebrates. In our study, it appears that the major effects of ENSO on aquatic macroinvertebrates are caused by ENSO-related changes in precipitation.

Influence of drought on community variability

Drought influenced the temporal constancy of communities. For example, at the first-order HKC sites, highest stability was observed during the 4 years (1988–91) of the prolonged drought, indicating that there was little change in the taxa present at that time. Furthermore, prolonged droughts tend to increase the constancy of wet-season flow conditions, and more stable flows should lead to more stable communities. For example, low community persistence and stability has been associated with high variability in discharge or low habitat stability (e.g. Bengtsson *et al.*, 1997; Oberdorff *et al.*, 2001). This pattern was not observed at the second-order sites (2P, 2D), or at site 1P in the dry-season. At these sites, the lowest stability coincided with the beginning of the drought period. In the second-order sites, high instability could be a result of a delay in the shift from a 'wet-year' to a 'dry-year' community because drought has less of an impact on flow in the larger streams (e.g. Bêche *et al.*, 2006). Furthermore, in the dry season, streams are more prone to desiccation during a prolonged drought, and intensified competition and predation could result in increased annual variability.

Capturing rare events: the importance of long-term data

The prolonged (HKC) and severe (Big Sulphur Creek, Blodgett Forest) droughts that occurred during the study periods were rare events. For example, an analysis of a long-term precipitation records (1895–2003) from northern California showed that only two other prolonged droughts (>3 years of precipitation >1 SD below mean) were comparable to that at HKC (1987–92, 6 years). These occurred in 1929–34 (5 years) and 1944–50 (7 years). Furthermore, the two most severe droughts on record include the HKC drought (<70% of average precipitation). At Big Sulphur Creek, 1977 was the driest year in the 108-year record (27% of average), and 1983 was the wettest year on record (174% of average). Similarly, the driest year in the 43-year record at Blodgett Forest was 2002 (42% of average), while the second-wettest year was 1995 (165% of average).

Because they are rare, extreme disturbance events such as the prolonged and extreme droughts examined in this study are often not captured in many ecological studies. However, some extreme (high

severity, low frequency) disturbance events result in both qualitatively and quantitatively different effects on ecosystems, indicating threshold effects (Romme *et al.*, 1998). In these cases, the disturbance effects cannot be extrapolated from smaller events. In this study, the effects of prolonged and/or severe drought on aquatic communities may not be predictable based on the effects of shorter droughts of smaller magnitude (Boulton, 2003) if thresholds are crossed (such as widespread habitat loss or aseasonal drying). For example, encroachment of vegetation during prolonged drought in the HKC sites resulted in a directional community change that was not reversed at all sites despite a return to 'average' and above-average precipitation.

Long-term studies are potentially able to capture a larger range of variability in environmental variability, which undoubtedly contributes to our understanding of community variability through correlational studies and lead to experiments to test hypotheses about the observed patterns. Furthermore, by encompassing a greater range of variability, we may be able to avoid false conclusions about community-environment relationships. For example, in a previous examination of a shorter period (1984–88) of the same HKC dataset, only two sites (2P, 2D) showed a significant relationship between total precipitation and taxon richness (Resh & Rosenberg, 1989). In this previous study, the lack of relationship in the first-order sites was attributed to reduced fluctuations in year-to-year discharge because of smaller catchment size. In the present study, however, all four HKC sites had significant precipitation-richness relationships, with the strongest relationships being in these smaller streams. Thus, the trends in taxon richness found with a shorter set of data, even from the same sites, led to a false conclusion. Such patterns are probably more widespread than we suppose (e.g. Scarsbrook, 2002), and they may have consequences for the applying biomonitoring tools to time periods not characteristic of the ones under which they were developed (e.g. applying a tool developed during 'wet' years to 'dry' years; Mazor, 2006).

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Appendix 1 Taxa occurring in at least 50% of all samples in each study region, as indicated by 'x' (Hunting and Knoxville Creeks: HKC; Big Sulphur Creek: BSC; Blodgett Forest: BFRS). Taxa codes correspond to NMS ordination plots in Fig. 4

Order/Higher	Family	Genus	Taxa code	HKC	BSC	BFRS	
Insects							
Coleoptera	Elmidae	<i>Lara</i>	Larasp			x	
		<i>Narpus</i>	Narpus			x	
		<i>Optioservus</i>	Optios		x		
Diptera	Staphylinidae	<i>Heterlimnius</i>	Heterl			x	
		<i>Stenus</i>	Stenus			x	
	Ceratopogonidae	<i>Palpomyia</i> sp. 1	Palpo1	x	x		
		<i>Palpomyia</i> sp. 2	Palpo2	x			
	Chironomidae	all sp.	Cerato			x	
		all sp.	Chiron			x	
		sp. 1	Chiro1	x	x		
		sp. 2	Chiro2	x	x		
		sp. 3	Chiro3	x	x		
		sp. 4	Chiro4		x		
		sp. 5	Chiro5	x			
		sp. 6	Chiro6	x			
		sp. 7	Chiro7		x		
		sp. 8	Chiro8	x	x		
		sp. 9	Chiro9	x	x		
		sp. 10	Chir10	x			
		sp. 12	Chir12	x			
		sp. 16	Chir16	x			
		Dixidae	<i>Dixa</i>	Dixasp			x
Empididae	<i>Chelifera</i>	Chelif			x		
Ptychopteridae	<i>Ptychoptera</i>	Ptycho			x		
Simuliidae	<i>Simulium</i>	Simuli	x	x	x		
Stratiomyidae	<i>Euparyphus</i> sp. 1	Eupar1	x				
	<i>Euparyphus</i> sp. 2	Eupar2	x				
Ephemeroptera	Tipulidae	<i>Antocha</i>	Antoch		x		
		all sp.	Tipuli			x	
	Baetidae	<i>Baetis</i>	Baetis	x	x	x	
	Ephemerellidae	<i>Ephemerella</i>	Epheme	x	x		
		<i>Serratella</i>	Serrat			x	
Megaloptera	Heptageniidae	<i>Cinygmula</i>	Cinygm			x	
		<i>Ironodes</i>	Ironod			x	
	Leptohyphidae	<i>Tricorythodes</i>	Tricor		x		
	Leptophlebiidae	<i>Paraleptophlebia</i>	Paralp	x	x	x	
	Sialidae	<i>Sialis</i>	Sialis			x	
Odonata	Coenagrionidae	<i>Argias</i>	Argias	x			
Plecoptera	Capniidae	<i>Paracapnia</i>	Paraca			x	
		<i>Sweltsa</i>	Swelts			x	
	Chloroperlidae	<i>Despaxia</i>	Despax			x	
	Leuctridae	<i>Malenka</i>	Malenk			x	
	Nemouridae	<i>Soyedina</i>	Soyedi			x	
		<i>Visoka</i>	Visoka			x	
		<i>Zapada</i>	Zapada			x	
		Peltoperlidae	<i>Yoraperla</i>	Yorape			x
		Perlidae	<i>Hesperoperla</i>	Hesprl			x
		Perlodidae	<i>Isoperla</i>	Isoper	x		x
	Trichoptera	Brachycentridae	<i>Micrasema</i>	Micras			x
		Helicopsychidae	<i>Helicopsyche</i>	Helico		x	
		Hydropsychidae	<i>Hydropsyche</i>	Hydrop	x	x	
			<i>Parapsyche</i>	Paraps			x
Hydroptilidae		<i>Ochrotrichia</i> sp. 1	Ochro1	x			
Lepidostomatidae		<i>Lepidostoma</i>	Lepido			x	

Appendix 1 (Continued)

Order	Family	Genus	Taxa code	HKC	BSC	BFRS
	Psychomyiidae	<i>Tinodes</i>	Tinode	x		
	Philopotamidae	<i>Wormaldia</i>	Wormal	x		x
	Rhyacophilidae	<i>Rhyacophila</i>	Rhyaco	x		x
	Sericostomatidae	<i>Gumaga</i>	Gumaga	x	x	
Non-insects						
Acarina			Acarin	x	x	x
Gastropoda	Planariidae		Planar		x	
Harpacticoida			Harpac			x
Mollusca	Sphaeriidae		Sphaer			x
Nematoda			Nematd	x		
Oligochaeta			Oligoc	x	x	x

Appendix 2 Spearman rank correlation (r_s) between each NMS axis and the measured physical variables for each region (all sites combined and separately)

	Axis	% var	Year	Total precip	1-mo precip	2-week precip	FST	Flow	SOI	SOI (lag)
Hunting/Knoxville Creeks										
All sites	1	34.9	-0.30*	-0.63*	-0.58*	-0.37*	-0.18	-0.22	-0.08	-0.03
	2	7.3	-0.27*	-0.13	-0.17	-0.04	-0.16	-0.40*	0.03	0.07
	3	39.2	0.16	0.23	0.09	0.25	0.73*	0.64*	-0.10	0.01
1D	1		-0.33	-0.69*	-0.63*	-0.28	-0.67*	-0.32	-0.28	-0.04
	2		0.01	-0.24	-0.50	0.01	-0.37	0.11	-0.38	-0.01
	3		0.50	0.21	-0.01	0.25	0.32	0.36	-0.22	-0.02
2D	1		-0.52	-0.70*	-0.61*	-0.47	-0.53	-0.71*	-0.15	-0.12
	2		-0.02	0.16	0.03	0.09	-0.46	0.01	-0.13	0.47
	3		-0.05	0.25	0.21	0.35	0.31	0.35	-0.12	-0.13
1P (wet)	1		-0.35	-0.68*	-0.67*	-0.54	-0.66	-0.59	0.01	-0.37
	2		-0.79*	-0.41	-0.39	-0.52	-0.59	-0.44	0.15	-0.01
	3		0.28	0.36	0.45	0.50	0.58	0.50	0.06	0.36
2P	1		-0.19	-0.80*	-0.72*	-0.44	-0.10	-0.68*	-0.02	0.19
	2		-0.20	-0.04	-0.04	0.15	0.60	-0.19	0.50	-0.02
	3		0.37	0.55*	0.20	0.57*	-0.20	0.44	-0.28	0.03
1P (dry)	1	41.6	-0.65*	-0.43	-0.41	-0.47	-	-	-0.36	-0.29
	2	46.9	0.02	0.03	-0.03	-0.28	-	-	-0.32	-0.18
	Axis	% var.	Year	Total precip	1-month precip	Flow	SOI	SOI (lag)		
Big Sulphur Creek										
All sites	1	20.6	-0.28	-0.58	-0.78*	-0.62	-0.13	0.22		
	2	14.3	0.66	0.19	0.13	0.27	0.34	0.34		
	3	45.8	-0.05	-0.70*	-0.59	-0.59	0.63	-0.33		
Riffles	1		-0.25	-0.43	-0.82	-0.46	-0.25	0.40		
	2		0.86	0.64	0.43	0.71	0.09	0.40		
	3		0.00	-0.71	-0.68	-0.61	0.59	-0.23		
Pools	1		-0.43	-0.79	-0.82	-0.89	0.05	0.07		
	2		0.68	-0.07	0.04	0.11	0.77	0.32		
	3		-0.18	-0.75	-0.64	0.64	0.63	-0.36		
	Axis	% var.	Year	Total precip	Flow	SOI	SOI (lag)			
Blodgett Forest										
All sites	1	25.2	-0.61*	0.57*	-0.42*	-0.29	-0.50*			
	2	57.4	0.68*	-0.71*	-0.60*	0.37*	0.63*			
	3	9.1	0.26	-0.38*	-0.06	0.37*	0.38*			

Appendix 2 (Continued)

	Axis	% var.	Year	Total precip	Flow	SOI	SOI (lag)
BC	1		-0.93*	0.81	0.93*	-0.40	-0.78
	2		0.86	-0.88	-0.84	0.36	0.86
	3		0.24	-0.43	-0.47	0.60	0.40
DC	1		-0.86	0.93*	0.73	-0.64	-0.71
	2		0.81	-0.83*	-0.83	0.60	0.76
	3		0.24	-0.40	-0.51	0.45	0.48
DE	1		-0.96*	0.75	-0.13	-0.18	-0.54
	2		0.75	-0.96*	0.28	0.43	0.61
	3		0.36	-0.43	0.80	0.36	0.75
GC	1		-0.83	0.76	0.21	-0.45	-0.88
	2		0.86	-0.90*	-0.55	0.55	0.93*
	3		0.07	-0.26	0.16	0.67	0.64
MC	1		-0.98*	0.81	0.22	-0.14	-0.67
	2		0.83	-0.95*	-0.11	0.50	0.88
	3		0.60	-0.67	0.33	0.48	0.62

Significant correlations are indicated in bold ($P \leq 0.05$) and/or with an asterisk ($P \leq 0.01$).